Plant Biotechnology Reports (2021) 15:259–278
https://doi.org/10.1007/s11816-021-00676-3

Online ISSN 1863-5474
Print ISSN 1863-5466

REVIEW

Perspectives for sustainable agriculture from the microbiome in plant rhizosphere

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Received: 19 March 2021 / Revised: 20 April 2021 / Accepted: 27 April 2021 / Published online: 13 May 2021

Abstract

The ever-growing human population globally has resulted in the quest for solutions to the problem of hunger by providing food security. The importance of plant-root-associated microorganisms cannot be overlooked, plants rely on them. These root colonizers dominate the rhizosphere due to the abundance of available nutrients, relying on their host plant for nutrients and other essential requirements. The relationships between microbial communities and plants are controlled by the type of plant and microorganism involved. Advances in modern molecular techniques have led to the evolution of omic technology using nucleic acid molecules to study plant-microorganism associations capable of stimulating plant growth, improve yield, and induce disease suppression. This review elucidates the activities of microbial communities, especially nitrogen-fixing rhizobacteria associated with plant roots, nitrogen fixation as a mechanism of promoting plant growth, their importance, and the challenges employing bioinoculants. Prospecting plant growth promoters using omic technology will advance sustainable agriculture globally.

Keywords Nitrogen-fixing genes · Omic technology · Plant growth-promoting rhizobacteria · Root nodulation process · Soil fertility

Introduction

Life dwelling on earth depends on the celestial environment and is controlled by the soil beneath our feet. Soil is a critical part of the ecosystem with valuable resources important to us, as the topmost layer of the earth; it holds plants at the root and support animal life. Above all, the soil is composed of numerous microorganisms interacting with each other. Soil ecosystem is a source of minerals, organic matters, liquids, and gases. Moreover, soil acts as a water filter and a medium that encourages plant growth (Beckers et al. 2017). All soil houses millions of organisms that contribute to the biodiversity and distribution of most of the antibiotics for fighting plant borne diseases (Zhou et al. 2020).

In the context of this review, the soil region around the plant root that connects the network of plant root-associated microorganisms, especially bacteria are found in the plant root system called the rhizosphere. Microbial communities in the rhizosphere perform dynamic beneficial interrelated functions in the plant root zone (Olanrewaju et al. 2019). The entire set of microbial populations inhabiting the plant root-associated region is referred to as the rhizosphere microbiome or rhizobiome. Some of these microorganisms may be pathogenic (harmful to plant growth) or non-pathogenic having symbiotic relationships with other rhizospheric microorganisms (Ali et al. 2017).

Lorenz Hiltner in 1904 introduced the term ‘rhizosphere’ due to Beijerinck’s discovery of bacterial community inhabiting the soil with the ability to fix nitrogen. According to the author, rhizosphere was described as root-associated soil compartment influenced by root activity. Furthermore, rhizosphere is the ecological niche where microorganisms dwell, serving as a connection to other plant root zones. Microorganisms in the compartment perform significant activities that contribute to plant health, mostly nitrogen fixation (Olanrewaju et al. 2019). The rhizosphere inhabits myriads of microorganisms and is considered a well-advanced external functional plant habitat, which is the plant’s second genome because plants are referred to as metaorganisms. Therefore, understanding the exact contributions of

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rhizobiome mainly nitrogen (N) fixing bacteria concerning plant health and productivity are important (Ali et al. 2017).

Bacterial species usually do not work in isolation but in association with other microbial species that have diverse beneficial impacts on plants, hence promoting plant growth or non-beneficial with damaging effects on the host plants (Bagyaraj and Ashwin 2017; Murphy et al. 2015). In the rhizosphere, the association between plant and the microbial communities occurs within the soil matrix (Pii et al. 2015; Sabale et al. 2019). Rhizosphere is a diverse habitat with a high abundance of microbial community called rhizobiome. The bacterial species are the most dominant microorganisms found in the rhizosphere, colonizing the microenvironment with mutual benefits (Bagyaraj and Ashwin 2017).

The beneficial rhizobiome in the regions have close interaction with host plants primarily contributing to the soil health for various agricultural purposes (Alawiye and Babalola 2019). Among other benefits of rhizobiome that are of attention is their interaction with other microorganisms and plants. Understanding the interactions in the rhizosphere is not solely for comprehending their involvement in plant growth and development. Likewise, to understand the different metabolic activities that occurs in the rhizosphere (Liu et al. 2015; Preece and Penuelas 2016). Also, for exploiting their association in phytoremediation approaches that can lead to the sustainable production of metabolites and crops (Schlemper et al. 2017).

More so, the microbial community control plant rhizosphere has led to competitors cohabiting in the environment in a mutual relationship (Liu et al. 2015). The positive relationship is a symbiotic relationship with the host plants or negative with damaging impacts that are from predators or pathogens (Igiehon et al. 2019). Either of the microbial community associations in the rhizosphere influence plant growth and tolerance to stressors, however, its significance is creating awareness (Rasmann and Turlings 2016).

Studies have shown that the rhizosphere is the hotspot for diverse abundance of microbial populations conducting several taxonomical operations. The root region (rhizosphere) is a complex soil environment that attracts much microbial mainly bacterial genera from the bulk soil. The bacterial community attracted to the plant root region interacts with the plant and other microbial communities, as a result, release metabolites for promoting plant growth. The plant roots and soil environment control the associations between microorganisms and plants as well as plants and microorganisms (Alawiye and Babalola 2019).

The rhizobiome play an essential role in sustaining and stabilizing the ecosystem. These roles influence the plant through gaseous and nutrient exchanges, and also, plant liter, water filter, and rhizodeposits. The plant root region is a path for nutrient and mineral absorption, which releases a several of organic and inorganic compounds known as rhizodeposits. The presence of rhizodeposits forms an exclusive environment in the rhizosphere, which serve as a pointer that diverse rhizobiomes are bound to be in abundance in the rhizosphere with high nutrients (Preece and Penuelas 2016).

Moreover, the rhizosphere contains a pool of microbial diversity conducting different interactions and functions, such as growth promotion and pathogen resistance. The rhizosphere is controlled by root exudates (low molecular weight organic compounds secreted by plant roots, which are released into the rhizosphere, capable of influencing the rhizosphere, inhibit harmful microorganisms, and promote plant growth), mucilages (polysaccharide substances extracted as gelatinous or viscous solution produced by most plants and some microorganisms), and border cells (those cells that separate from plant root tips and disperse into soil environment) released into the rhizospheric soil by plant roots.

Plants secrete border cells, exudates, rhizodeposit nutrients, and mucilages that attract microorganisms to the region, which serve as food for microorganisms inhabiting in the rhizosphere. The rhizosphere is structured by groups of microorganisms mostly bacterial species that are mesmerized by the rhizodeposits disseminating from the plant roots (Orlikowska et al. 2017). Ultimately, contributing to making the soil the most complex and diverse habitat in the ecosystem to a point that many microbial species colonizing the rhizosphere release regulatory substances that can influence plant ability to survive in challenging soil environmental conditions, including in waterlogged areas, extreme cold or desert on the planet that is a threat to sustainable agriculture (Alawiye and Babalola 2019; Sabale et al. 2019).

Sustainable agriculture is an integrated farming system having a site-specific approach that would over time satisfy the human need for food, improve environmental quality, and natural resources. Generally, improve the economy, result in enhancing the farmers and society in the quality of life. Sustainable agriculture relies on fertile soil, but rapid desertification and land degradation have damaged the soil caused an approximate loss of about 24 billion tons of fertile arid land world-wide (Pii et al. 2015; Zhou et al. 2016).

Plant microbial communities participate in transformations that impact on the composition of litter, which could lead to some changes in the turnover of nutrients, soil structure, physiology, and characteristics. These might cause changes in the structure and composition of plant microbial communities (Xu et al. 2019). In addition, biotic and abiotic factors control the microbial activities in the rhizosphere region. The rhizobiome coexisting in the rhizosphere plays an essential role in improving soil quality, plant health, and crop production (Zhang et al. 2017).

The inoculation of diverse bacterial species into the soil helps in improving plant-microorganism interactions, biogeochemical cycles, and biological engineering. Therefore, could encourage agriculturists from the application of agrochemicals, substituting the functions of these toxic chemical-based products for suitable beneficial bacteria (Li et al. 2019). The overall understanding of the biodiversity and structure of functional and active root and free-living microorganisms in the rhizosphere, such as nitrogen-fixing bacteria, capable of fixing nitrogen for plant use, which is paramount in enhancing crop performance and growth, in turn, increase agricultural crop production (Lagos et al. 2015).

To gain a complete understanding of the microbial network in the rhizosphere, it is necessary to integrate the interactions between the most abundant soil, and plant root microorganisms (Zhou et al. 2020). A detailed review of the interactions of the diverse nitrogen-fixing microbial community in the rhizosphere was discussed. Also, a comprehensive review of the mechanism of nitrogen fixation, contributions, and challenges of applying PGPR in sustainable agriculture was discussed. Conclusively, omics techniques for identifying and characterizing microbial communities were highlighted.

Rhizobiome of agricultural plants: plant growth promoters

Rhizobiome referred to as rhizobacteria are a class of bacterial species found in the rhizosphere with the ability to enhance host plant growth. Plant growth is stimulated by diverse microbial communities present in the rhizosphere. Several plant growth-promoting microorganisms are cohabiting in the rhizosphere. Plant root assembles many plant growth-promoting rhizobacteria communities such as *Azospirillium*, *Rhizobium*, *Arthrobacter*, and *Pseudomonas* into the internal, surface of plant roots, and surrounding the plant environment (Lagos et al. 2015).

The rhizobiome play critical beneficial roles in the host plant, including plant nutrient cycling, phytohormone production, and immunity against phyto-pathogens., couple with, the specific capacity to further improves soil fertility (Lee et al. 2019). In this instance, the plant microbial community has been described to accouter plant hosts with new pools of genes attributed as extended genome or plant genome (Igiehon et al. 2019; Vandenkoornhuyse et al. 2015). Meanwhile, some scientists have reported the richness of rhizobacteria in plant root regions and rhizospheric soils. Hence, any shift in the balance or changes in the edaphic conditions will certainly have impact on the soil microbiota and crop yield (Lee et al. 2019). Various agricultural beneficial microorganisms and their functions in the rhizosphere of different plants are outlined in Table 1.

Recently, the attentions of some scientists have been drawn to the critical effects of plant growth-promoting rhizobacteria (PGPR) on plants. The impacts have unveiled the different mechanisms of interactions between plants and bacterial communities in the rhizosphere. PGPR has been identify as a means to enhance sustainable food production in the future (Babalola 2010; Finzi et al. 2015; Igiehon et al. 2019). Various mechanisms are employed by PGPR to either promote plants growth or have general impact on the plants, for example, the production of inhibitory substances (antifungal and antibiotics metabolites) against plant pathogens (Igiehon et al. 2019; Vandenkoornhuyse et al. 2015). In particular, *Firmicutes*, *Proteobacteria* and *Actinobacteria* are involved in suppression of diseases caused by the pathogenic fungus *Rhizoctonia solani*. Another study showed that certain bacteria were able to eliminate the impact of *R. solani* on lettuce, further suggesting that some bacteria have impacts on rhizosphere-assocaited bacteria and plant tissue-associated fungi (Scherwinski et al. 2008), especially the pathoegenic ones. Another example is *Pseudomonas* sp. AF-54 isolated from sunflower rhizosphere with antagonistic effects on *Fusarium* sp. The bacterium can be a promising biocontrol agent against sunflower pathogens (Majeed et al. 2018a). It was however shown that beneficial bacterial species, such as *Pseudomonas fluorescens* F113, produce antifungal substance 2, 4-diacetylphloroglucinol that are not detrimental to the mycorrhizal fungus *Glomus mossea*, but rather helps the fungus to colonize host plants' roots more effectively (Barea et al. 1998). On the other hand, like bacteria, certain fungi can contribute to mycorrhizal root colonization while they hamper the growth of other fungi in the rhizosphere (Igiehon and Babalola 2018b), meaning that, there are some fungal species that inhibit the growth and/or survival of other fungi in the soil ecosystem.

Other mechanisms of PGPR are mainly through biogeochemical cycles, significantly in the nitrogen fixation process by nitrogen-fixing bacterial species, which specifically possess nitrogen-fixing genes (*nif*) that provide nitrogen for usage (Chen et al. 2019a; Igiehon et al. 2019) by plants, especially nodule-forming plants. The process involved in the formation of nodules has been reviewed in detailed in previous studies (Igiehon et al. 2018a; Oldroyd et al. 2011; Udvard and Poole 2013). However, some bacteria cannot initiate nodulation process since the process entails complex plant-microbial interactions. Some nitrogen fixing bacteria contribute to nitrogen fixation process for host plant development by penetrating root cracks and/or wounds possibly created by root movement within the soil (Gaiero et al. 2013; Santi et al. 2013). *Azoarcus* sp. BH72, which is a kallar grass root tissue-associated bacterial species improved the dry weight of the grass when grown in nitrogen-deficient soil compared to the '*nifk* mutant strain of BH72'. Nevertheless, the bacterial species can mutate from free-living to endophytic, as well as from endophytic to free-living forms. Also, soybean plants inoculated with *Rhizobium* spp. alone and co-inoculated

Table 1 Some plant root-associated microorganisms and their influence on plants

Microorganisms	Effects (Positive and negative)	References
Burkholderia sp., *Achromobacter* sp., *Azospirillum* sp., *Chryseobacterium* sp.	Stimulatory effects on plant growth	(Ambrosini et al. 2015)
Rhizobium spp. YAS34	Promote plant growth under stressed conditions, and resistance to water Make use of fertilizer more effectively by increasing nitrogen uptake	(Ali et al. 2017)
Proteobacteria, Acidobacteria	Indicates soil nutrient	(Beckers et al. 2017)
Azotobacter vinelandii; Azotobacter Chroococcum	Promote plant growth	(Ali et al. 2017)
Frankia	Nitrogen-fixing, and P-solubilization	(Beckers et al. 2017)
Candidatus Saccharibacteria	High indicator: To biotic and abiotic stresses; strict nutrient requirements; plant innate immune responses; Interact with host plant genotype and microorganism-to-microorganism interaction	(Starr et al. 2018)
Azospirillum lipoferum	Inhabits plant root niche and crude oil contaminated soil	(Singh et al. 2018)
Enterobacter	Produces siderophore, Indole Acetic Acid (IAA), and HCN; Fixes nitrogen, and P-solubilization	(Starr et al. 2018)
Pyrococcus furiosus, Flavobacterium	Biocontrol activity; P and K solubilization	(Singh et al. 2018)
Bacillus ceres	Causes rootlet rot	(Singh et al. 2018)
Curtobacterium,	Phosphorus solubilization, and IAA production	(Ali et al. 2017)
Pseudomonas putida GR12-2	Ethylene, and ACC-deaminase inhibitor	(Alawiye and Babalola 2019)
Pseudomonas fluorescens angstrom 313	Causes shunted growth in plant	(Mosimann et al. 2017)
Bacillus substilis	Causes sour skin, and soft-rotting disease of onion	(Murphy et al. 2015)
Pseudomonas fluorescens; Pantoea agglomerans	Antifungal activity	(Alawiye and Babalola 2019)
Azospirillum brasilense	Promotes the uptake of NO3, K + , and H_2PO_4	(Ali et al. 2017)
Burkholderia ambifaria MCI7	Antifungal activity, siderophore production, Increase shipped weight, and plant performance	(Mosimann et al. 2017)
Burkholderia pseudomallei	Causes melioidosis	(Manivanh et al. 2017; Mora-Ruiz et al. 2018)
Halobacillus sp	Biocontrol activity, IAA production, and P-solubilization	(Mosimann et al. 2017)
Pseudorhodoplanes, Paenibacillus, ocuria	Indole Acetic Acid production, P-solubilization, and nitrogen-fixing	(Şeker et al. 2017)
Arthrobacter	P-solubilization, production of IAA, and biocontrol Agent	(Singh et al. 2018)
Pseudomonas fluorescens, and *P. fluorescens* biotype F	ACC deaminase activity, Chitinase activity; increased grain yield, and weight	(Şeker et al. 2017)

with *Rhizobium* spp. and mycorrhizal fungal consortium were observed to nodulate the plants in the field at North-West Province of South Africa under semi-arid condition (Igiehon et al. 2020). The *Rhizobium* spp. were shown to possess *nif* and *nod* genes upon analyses of their whole genomes through Kbase pipeline (Igiehon et al. 2019, 2020).

Chen et al. (2019b) studied PGPR communities of wheat plants and their beneficial effects on plant development. The results provided insights that proved a shift in root rhizobiome can affect plants and the microbiome. There are shreds of evidence that has of course implicated the activities in the rhizosphere that trigger the release of rhizodeposits that are of benefits to plant. So to traditionally observe the effects of various cultivated plants on the composition of PGPR found in the rhizosphere, there is a need to understand the abundance and activities of the PGPR in rhizospheric soil (Babalola 2010; Chen et al. 2019a; Hu et al. 2018).

The activities of the PGPR determine the number of organic compounds excreted by the roots. Thus, these compounds are collectively known as exudates (Babalola 2010; Hu et al. 2018). The exudates and other rhizodeposits influence the physical and chemical structures of the rhizobacteria (Cregger et al. 2018). PGPR assimilate and released exudates deposits, the exudates are then discharged into the rhizospheric soil after modification (Crawford and Knight 2017). In return, it is important for the soil quality that increases when these deposits are absorbed by the PGPR that can finally boost plant growth (Orlikowska et al. 2017). For example, root polysaccharide enhanced the production of biofilm matrix by *Bacillus subtilis*, this rhizobacteria is of benefit to plants generally (Olanrewaju et al. 2019). Figure 1 outline the different mechanisms of action PGPR uses in improving plant growth.

PGPR perceives different signals secreted from plant roots. Ultimately, it releases different signaling molecules that control various stress responses that are caused by edaphic conditions. This usually equips the plant with the ability to resist or tolerate the different stresses that would lead to root development, plant growth, and increase in crop productivity (Crawford and Knight 2017; Lyu et al. 2019). PGPR coexisting in the rhizosphere respond differently to root metabolic activities by stimulating biomass and activities (Lyu et al. 2019).

The growing pieces of evidence in the study of plant growth promotion have proved that PGPR improves soil health and quality, for this reason, promotes plant development and growth. For example are PGPR that speeds up nutrients cycling, influences, increases available nutrients, and nitrogen-fixation (Finzi et al. 2015; Lyu et al. 2019). Adding further, the PGPR does not perform activities in isolation, there is an association between the plant and microbiota in the micro-environment. This coexistence influence seedling survival that results in the advancement of plant growth performance and productivity (Crawford and Knight 2017).

There are shreds of evidence that backs up the competence of PGPR in sustainable agriculture. Nevertheless, PGPR was first explored only for improving crop production

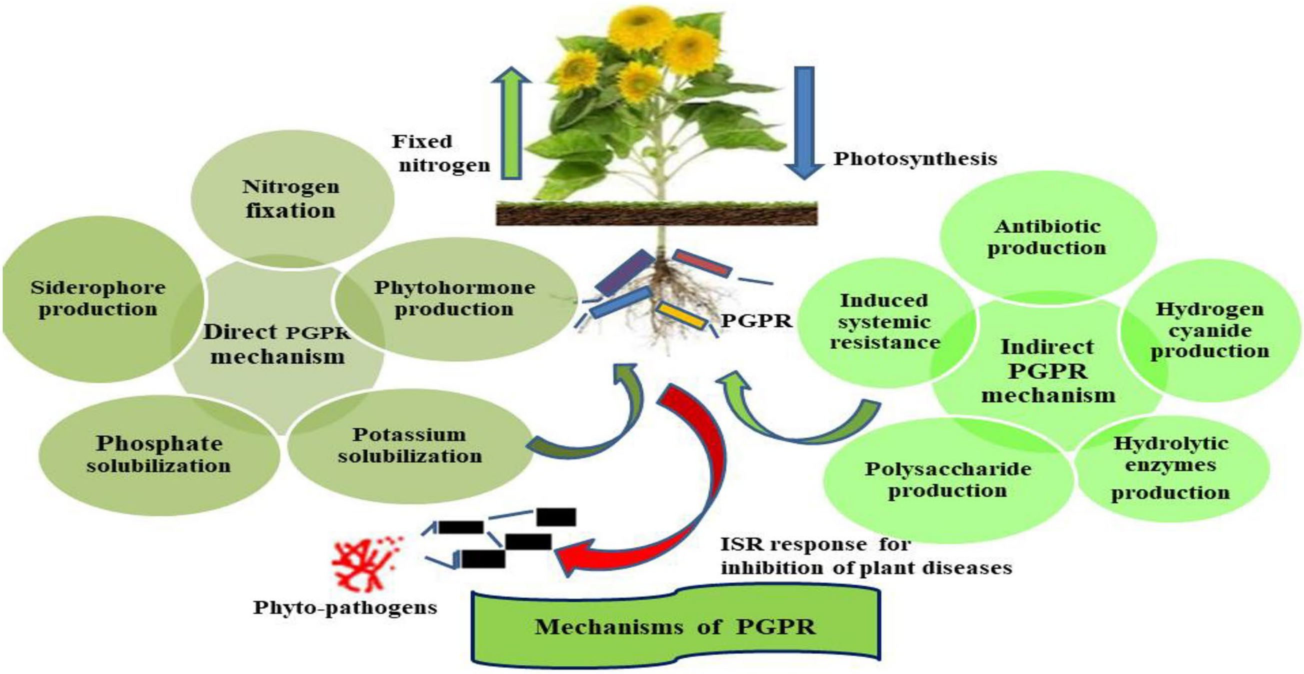

Fig. 1 Mechanisms of plant growth promotion. PGPR promotes plant growth by direct and/or indirect mechanisms. The direct PGPR mechanism includes nitrogen fixation, siderophore production, phosphate solubilization, potassium solubilization and phytohormone production, while the indirect PGPR mechanism includes antibiotic production, hydrogen cyanide production, hydrolytic enzyme production, polysaccharide production and induced systemic resistance. The PGPR also helps the plant to fight against phyto-pathogens. PGPR stands for plant growth promoting rhizobacteria, while ISR stands for induced systemic resistance

(Lyu et al. 2019). Recently, it has been proposed that it plays a critical role in the suitable functioning of the agroecosystem (Oak 2019). Scientists have shown that PGPR is beneficial for the improvement of soil quality, combating pathogens, and the effects of climate change. Identically, it can help in the restoration of degraded land and decrease the effects of environmental soil pollutants (Lyu et al. 2019). Evidently, Majeed et al. (2018b) recorded different strains of *Pseudomonas fluorescence* and *Pseudomonas* sp. strains, for example, *Pseudomonas* sp. AF-54 from sunflower rhizosphere as promising microorganisms with plant growth-promoting traits.

Other agmricultural beneficial microorganisms present in the rhizosphere are mycorrhizal fungi (MF), which have pesticidal genes that could destroy the negative effects of chemical-based pesticides applied on soil and indirectly enhance plant biomass (Bulgarelli et al. 2015). Few of the agricultural important fungal strains that provide mineral nutrients for plants are genera frequently isolated from the root region in high abundances, such as *Fusarium*, *Xylaria*, *Cladosporium*, *Dactylonectria*, and *Trichoderma* (Muller et al. 2018). Although, there are reports on some fungal genera in low abundance, for example, *Aspergillus*, *Alternaria*, *Mucor*, *Leptoxyphium*, and *Chloridium* (Crawford and Knight 2017; Lee et al. 2019; Pelagio-Flores et al. 2017).

However, not only the rhizobacteria and AM are the members of the rhizobiome present in the rhizosphere. Other microorganisms cohabiting in the rhizosphere have been documented. Lee et al. (2019) identified and reported an abundance of archaea groups commonly known as ammonium oxidizers in the rhizosphere than the bulk soil. Some phyla of archaeal from the rhizosphere of the tomatoes plant recorded are *Aenigmarchaeota, Crenarchaeota*, *Diapherotrites*, *Euryarchaeota*, *Pacearchaeota*, *Woesearchaeota,* and *Thaumarchaeota.*

Plant root-bacterial interactions in the rhizosphere

Plant root plays different essential roles, including anchoring and supporting of the plant to the ground, absorption of water, inorganic nutrients, and food. Additionally, nutrient storage, translocation of minerals and water to the stem; secretion and accumulation of various potential compounds, such as the secondary and primary metabolites peptides, sugars, carboxylic acids, and proteins (Kuzyakov and Blagodatskaya 2015). The underground world of plants is a network of interactions facilitated by the microbial community and plant roots. The plant root regions and soil are colonized by arrays of bacteria that promote the symbiotic relationship, resulting in the enhancement of nutrients bioavailability and the release of organic substances into the habitat (Beckers et al. 2017; Nwachukwu et al. 2021).

In our previous study Nwachukwu et al. (2021), the effects of plant roots on rhizosphere bacteria was reported to have been caused by root length, volume, biomass and surface area. These root-associated parameters encourage the bacterial species to interact in the rhizosphere (Phour et al. 2020). These interactions can be in different forms including antagonism, parasitism, amensalism and symbiosis, which play a critical role in providing the host plants with different benefits (Igiehon and Babalola 2018b), thereby contributing to the sustenance of the plants. Also, these microbial interactions in the rhizosphere is relevant to agriculatural practices that depend less on chemical fertilizer applications.

The relationship between plant root and bacteria was first recorded by Foster and Rovira in 1976, they considered different ultrathin sections of the wheat bacterial community with the aid of a transmission electron microscope (Kuzyakov and Blagodatskaya 2015). The result showed that bacteria sparsely colonized immature roots in the root regions. Conversely, in the cortical cells and cell walls, rhizobiome were more abundant. Correspondingly, in an experiment, it was reported that bacterial species in the rhizosphere had a significant difference compared to the bacteria in the bulk soil in different capacities, including numbers, types, and sizes (Muller et al. 2018). Contrary to what was reported, abundant bacterial species in the tomato plant endosphere compared to other niches studied (Zhou et al. 2016).

Recently, in a study, bacterial genera of more beneficial functional impact were abundant in the rhizosphere. The abundant bacterial genera were *Alphaproteobacteria*, *Firmicutes*, and *Actinobacteria.* Outside the rhizosphere, *Verrucomicrobia* were higher in the bulk soil compared to other niches (Lyu et al. 2019). However, there was a disparity in the results of a related study on soybean plant rhizosphere. A group of bacterial communities with a particular nutritional function was abundant in the root surface or rhizoplane while the least was in the surrounding bulk soil (Lee et al. 2019; Zhou et al. 2020).

Besides, the metabolism of nitrogen, potassium, and phosphorus, the bacterial community is involved in iron metabolism and uptake, also transportation of membranes (Fonseca-García et al. 2016). The diversity of bacterial communities that colonize the different below ground zones has been comprehensively studied to interpret the mechanisms that allow various interactions between the internal tissues, root surface, rhizosphere, and bulk soil. Varieties of substrates are released through organic nutrients and growth-promoting materials that bacterial species act on, resulting in the promotion of plant growth (Tassi et al. 2017). Plants dispense peculiar organic substrates that are utilized by bacteria. Hence, it provides inorganic nutrients and growth-promoting substances that stimulate plant growth.

Accordingly, Singh et al. (2019) isolated different species of rhizobacteria possessing multiple plant growth-promoting traits from sunflower rhizosphere soil. The interaction between PGPR and other resident microorganisms produced secondary metabolites with plant growth-promoting properties. Some of the rhizobacteria was member *Bacillus subtilis* strain Rhizo SF48, *Bacillus thuringiesis* strain Rhizo SF 23, *Acinetobacter* sp. strain N15254. Also, various strains of *Pseudomonas* and *Enterbacteria* spp were reported. Some of the identified PGPR inhibited the growth of *Fusarium oxysporum*.

Several factors, such as soil properties and type, plant genotype, different plant developmental stages, and rhizodeposits influence the level of interactions between bacterial communities and plant root systems (Beckers et al. 2017). The different interactions that occur in the rhizosphere produce various available rhizodeposits, including those that depend on different abiotic and biotic factors; plant variants and developmental stages (Beckers et al. 2017; Lagos et al. 2015). Although the upper part of the plant is held by soil at the root, plants need a variety of macro and micronutrients that play beneficial roles for their growth and development. Some nutrients are required in major quantity and are called macronutrient, namely, nitrogen, carbon, sulfur, calcium, and phosphorus. However, some nutrients are needed in smaller portions which are referred to as micronutrients, for example, zinc, iron, magnesium, and nickel (Finzi et al. 2015; Fonseca-García et al. 2016).

Moreover, toxic elements, such as heavy metals in the soil have been reported to get accumulated in plant tissues over time, when present in extreme conditions and above the permissible limits, for example, barium (Finzi et al. 2015). The negative impact of the presence of toxic elements in the soil is that it becomes toxic to plants as a result limit plant growth. Ordinarily, a high amount of toxic elements within plant tissues have a direct or indirect impact on the plant (Beckers et al. 2017). The direct impacts generate oxidative stress that increases the inhibition of cytoplasmic enzymes and damages the cell structures (Vandenkoornhuyse et al. 2015). The indirect impact substitute's nutrients that is essential to plant cation exchange sites. In that case, the ions control the roles of different enzymes and proteins. Thereby, stops metabolism and reveals the extent of toxicity in the plant, for example, ions (boron) which have been reported to be toxic to plant even at low concentrations (Tassi et al. 2017).

Soil fertility: role of PGPR

The soil is a habitat for various macro-organisms, such as ants, earthworms, insects, termites, and with a substantial number of microorganisms that participate in nutrient cycling, mineralization of organic compounds, synthesis of phytohormones, and other important processes that advance plants productivity. Furthermore, they help in improving and maintenance of soil fertility (Susilowati et al. 2015).

PGPR colonize plant roots and have been implicated in all important activities that occur in the soil such as the promotion of plant health by the aiding plant take-up in many nutrients. In addition, control the pathogens that could affect the host plant negatively. The moisture content in the soil determines the colonization of PGPR in the rhizosphere and long-term soil fertility. PGPR is responsible for synthesizing many biomolecules that enhance soil health (Vandenkoornhuyse et al. 2015).

Several organic compounds that operate as plant residues undergo decomposition and mineralization. These minerals increase soil health and fertility (Fig. 2). The high amount of phosphate available to plants is as a result of P solubilization, an activity performed by PGPR. Additionally, other chemicals in charge of plant growth are formed and they influence the plant root morphology and enhance soil health and fertility. The soil environments are improved mainly by bacteria species thus readily makes nutrients available (Suyal et al. 2015). The presence of nitrogen (N) in plants is critical for protein and amino acid synthesis. Nitrogen is acquired from the atmosphere, rhizosphere, and soil through the fixing of nitrogen. However, volatile compounds and metabolites are released by PGPR to improve plant and soil health (Igiehon et al. 2019).

Likewise, different enzymes are released to control the increase and effect of pathogens, hence contribute to the biocontrol of phytopathogens and improvement of plant growth. These compounds boost crop yield and enhance soil health. The overall mechanisms are essential to achieve a more fertile soil (Jiang et al. 2016). Apart from promoting plant growth, PGPR inoculant as a biofertilizer could enhance resident soil microbial diversity without causing any harm in the soil or to humans, unlike the traditional chemical-based fertilizers that have been implicated in the contamination of farmland after application. For example, nitrate from chemical fertilizer capable of contaminating below groundwater, which can run-off from the soil after rainfall and contaminate the surface water.

Interestingly, some PGPR acts as both biopesticides and biofertilizers, for example, *Burkholderia cepacia*. A study on maize showed that these microorganisms stopped the negative impact of *Fusarium* species and promoted maize growth in iron-deficient soil by producing siderophore. Some PGPR species produce siderophore and antibiotics with antagonizing properties that could stimulate systemic resistance, which may suppress the impacts of many pathogens which can be used for many agricultural purposes, including improving soil fertility (Manivanh et al. 2017).

Additionally, arbuscular mycorrhizal fungi having plant growth-promoting and pesticidal traits have been recorded as a beneficial rhizospheric microorganism with the potential

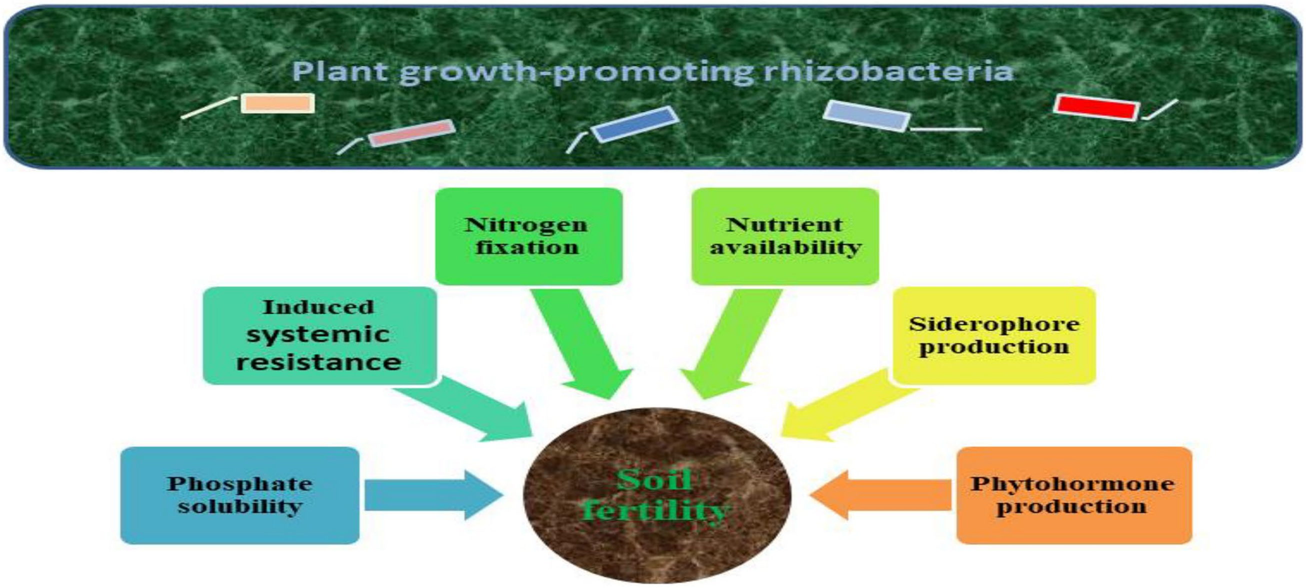

Fig. 2 Contributions of plant growth-promoting rhizobacteria to enhance soil fertility. Plant growth promoting rhizobacteria contribute to soil fertility by fixing atmospheric nitrogen (nitrogen fixation), enhancing iron availability through siderophores production, enhancing nutrient availability through phytohormone production and phosphate solubility, as well as priming the defense mechanisms of host plants to improve resistance against wide range of phyto-pathogens

of destroying the damaging effects of chemical fertilizers, resulting in increased plant biomass and improve soil fertility significantly proves that AMF is a promising microorganism for sustainable agriculture. Jadhav and Anil (2020) reported the influence of AMF on soil fertility and sunflower plant growth. Therefore, it is important to harness agricultural beneficial rhizobiome with the potential of enriching agricultural soil for sustainable agricultural development.

Biological nitrogen fixation: PGPR as nitrogen fixers

The rhizosphere is made up of a unique and enormous variety of bacterial species. Some are cultivable and known (1%), while 99% are yet uncultured, which makes it challenging for researchers to assess them. The variations of bacterial communities mainly PGPR, shape the integral structure of the rhizosphere (Alawiye and Babalola 2019; Igiehon and Babalola 2018a). According to Olanrewaju et al. (2019), a large proportion of bacteria colonize different land plant roots and niches. These bacteria are assembled to make up the rhizobiome.

Among the plant root microenvironment the rhizosphere is a thin soil layer that surrounds plant roots, hence acts as crossroads for microbial interactions, which makes this zone an exceptionally special, active, and important zone with the potential for diverse root activities and unique metabolic processes (Zhou et al. 2020). Rhizobacteria communities co-existing in the rhizosphere are plant growth promoters that play several roles, including nitrogen fixation, increasing available nutrients, phytopathogens suppressions, and disease inhibitions. Again, improve plant persistence and tolerance to environmental stress, such as high salinity and water shortage (Babalola 2010; Olanrewaju et al. 2019).

Rhizosphere as a haven for diverse bacterial species with a unique structure and composition that is impacted by plant regulated mechanisms (Mukhtar et al. 2019). Variations in the rhizosphere are modified by most bacterial populations broadly advantageous to plants (Bulgarelli et al. 2015; Lee et al. 2019). Recently, there were detailed reports documented on rhizosphere, bacterial components, and their influence on plants (Kuan et al. 2016; Mukhtar et al. 2019). It has been recorded that in the rhizosphere, nitrogen-fixing is the fundamental mechanism that enhances plant growth (Lee et al. 2019; Susilowati et al. 2015).

Nitrogen (N) is a major macronutrient important for the growth and productivity of all living organisms, bacteria, and plants inclusive. Nitrogen is found in membrane lipids and nucleotide (Mukhtar et al. 2019; Zhang et al. 2017). It is among the major essential component of plant dry mass because it is the main constituent of chlorophyll (compound plants use from sunlight to produce sugars from water and carbon dioxide) and amino acids. When plants do not get enough nitrogen, they are unable to produce amino acids, without amino acids plants cannot make the unique protein that plant cells require for growth (Babalola 2010).

The biological fixing of atmospheric nitrogen is an essential microbial activity that supports life on earth. This process takes place when atmospheric nitrogen is transformed to ammonia (NH_3) by a highly complex oxygen unstable enzyme system found in free-living symbiotic diazotrophs called nitrogenase (Igiehon et al. 2019). Nitrogen fixation is an energy-demanding process that requires the hydrolysis of a minimum of 16 mol of ATP per mole of reduced nitrogen (Souza et al. 2015). Taking into consideration the two kinds of nitrogen fixation (symbiotic and non-symbiotic) base on the category of related organisms and plant involved.

Gram-negative rhizobacteria species possessing plant growth-promoting traits capable of fixing nitrogen dominated the rhizosphere, these categories of rhizobacteria can be referred to as nitrogen fixers (Alawiye and Babalola 2019; Igiehon and Babalola 2018a). The common range of nitrogen-fixing rhizobacteria genera with the potential of improving plant growth and development, which consequently lead to increase in crop productivity, include *Azospirillum*, *Azotobacter*, *Acetobacter*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Serratia*, *Pseudomonas*, and *Mitsuaria* (Babalola 2010; Bagyaraj and Ashwin 2017; Manivanh et al. 2017). Other important rhizobacteria strains such as *Pseudomonas fluorescens* Pf153 and *Pseudomonas* sp. DSMZ 13,134 from a particular locality having different plant growth-promoting traits with influence on maize crop yield was reported by Mosimann and teammates (2017). Correspondingly, *Vibrio fluvialis* NWU37, *Pseudomonas fluorescens* NWU65, and *Ewingella Americana* NWU59 were identified in our laboratory, likewise *Streptomyces* species and lots of *Proteobacteria* (Alawiye and Babalola 2019).

The common broad range of nitrogen-fixing bacteria present in the rhizosphere, which symbiotically fix nitrogen with a particular plant is *Pseudomonas, Rhizobium, Frankia, Azotobacter Paenibacillus, Klebsiella*, *Salinibacter, Festuca juncifolia*, *Agrostis capillaris*, *Holcus lanatus*, *Poa pratensis*, *Bradyrhizobium, Sinorhizobium, Mesorhizobiu*, and *Deschampsia cespitosa* in synergistic association with leguminous and non-leguminous plants and trees that employ their functions (Kuan et al. 2016; Mukhtar et al. 2019). Distinct features are used to differentiate members of nitrogen-fixing bacterial communities in various plant rhizospheres. Some plants inhabit different nitrogen-fixing bacterial communities, such as sunflower (Majeed et al. 2015a), rice (Miller 2018), poplar (Mukhtar et al. 2019), halophytes (Mora-Ruiz et al. 2018), *Arabidopsis* (Ali et al. 2017), and Tomato (Lee et al. 2019).

A study of different plant varieties reported that the genus *Pleomorphomonas* known for their nitrogen-fixing capacity was abundant in the rhizosphere (Kang et al. 2019). Similarly, Ambrosini et al. (2018) recorded nitrogen-fixing *Bacilli* belonging to the genus *Paenibacillus* spp from the sunflower rhizosphere. Many processes trigger bacterial-plant interactions, which have led to the development of beneficial relationships and have enhanced adjustments to different environmental challenges (Pii et al. 2015). Another, distinct nitrogen-fixing bacterial species from the rhizosphere plant root system of mature *Populus deltoides* trees have been reported (Salas et al. 2017).

Notably, non-symbiotic bacteria fix the fewer amount of nitrogen, sufficient to the associated host plants compared to bacteria found in the root nodule (rhizobia) (Mosimann et al. 2017). Despite the slower fixing capability of non-symbiotic bacteria, few PGPR has proved to be very efficient in increasing this process by making the nitrogen nutrient that is short in supply accessible to plants. During a non-symbiotic nitrogen-fixing activity, free-living diazotrophs excite the growth of non-leguminous plants.

The common genera of this group are *Anabaena*, *Diazotrophicus*, *Azotobacter*, *Azocarus*, *Cyanobacteria*, and *Gluconoacetobacter diazotrophicus* (Zarraonaindia et al. 2015; Zhang et al. 2017). The application of cultures with non-symbiotic nitrogen-fixing PGPR, mainly *Azospirillum* and *Azotobacter* enhanced the productivity of crops (Pii et al. 2015; Souza et al. 2015). Just as *Rhizobium* nitrogen fixation is important in the cultivation of various plants (Ambrosini et al. 2012; Jadhav and Anil 2020). Ambrosini et al. (2018) reported that novel nitrogen-fixing *Paenibacillus helianthi* sp. nov. encouraged high growth and yield of sunflower plants.

The majority of rhizospheric nitrogen-fixing bacterial species populate the host plant root, some may emanate from other tissues, such as internal tissues, leaf, flowers, and bulk soil (Salas et al. 2017). A high abundance of members from the phyla *Proteobacteria* and *Spirochaetes* were identified from the rhizosphere and bulk soils of rice farm, whereas *Gemmatimonadetes*, *Acidobacteria,* and *Planctomycetes* were in depletion (Miller 2018).

Among the nitrogen-fixing bacterial communities in the rhizosphere are bacteria that colonize the host plant root by establishing themselves in the root surface, while a fraction finds their way into the plant's internal tissues and is controlled by the innate immunity of the plant (Jiang et al. 2016). Some phyla recorded within the root surface and internal tissues are Alpha, Beta, and *Deltaproteobacteria.* Few indicated classes are *Chloroflexi* and *Bacteroidetes* (Li et al. 2019; Miller 2018).

Bacterial communities in the rhizosphere use of a wide variety of substances that increase the higher colonization and persistence rates serving as sources of the nutrient (Crawford and Knight 2017; Cregger et al. 2018). The rhizoplane, which is the plant root surface is one of the plant root systems where bacteria inhabit and attach themselves to the root surface structures with the aid of either the cell surface polysaccharides or fimbriae or flagella (Miller 2018; Olanrewaju et al. 2019).

Similarly, some reports stated that there is a fragile boundary between the rhizoplane and rhizosphere (Beckers et al. 2017; Mukhtar et al. 2019; Olanrewaju et al.

2019). Before now, researchers have recorded that some nitrogen-fixing bacterial species, such as *Caulobacter* sp. and *Zoogloea ramigera* identified from rhizoplane of some plants (Beckers et al. 2017; Edwards et al. 2015). These bacterial species are capable of controlling the nutrient status of the surrounding soils and other factors, such as pH (Elmagzob et al. 2019).

Most scientists have overlooked the activities occurring in the internal tissues (endosphere), which makes this region the least studied. Endosphere is a plant microenvironment that harbours a lesser concentration of bacterial communities called endophytic bacteria (Gomes et al. 2018; Zhou et al. 2016). The interior root region being an exclusive niche has a fewer number of bacterial density compared to the root surface (rhizoplane) while rhizosphere has more abundant bacterial diversity (Elmagzob et al. 2019). Table 2 describes nitrogen-fixing genes and the functions.

The beginning of molecular communication between soil bacterial and host plants occurs through the discharge of signals as communication chemicals, for example, flavonoid capable of improving plants-microorganism relationship (Alawiye and Babalola 2019; Ali et al. 2017; Carrell and Frank 2015). Majeed et al. (2018b) recorded that this chemical helped in the choice of the greater befitting partners for their development and the destruction of the pathogenic once. The communication signal is recognized by NodD (bacteria receptor) which acts as a transcriptional activator of nodulation genes (NodA, NodB, NodC, and NodFE). Evidently, Nod factors stimulate agent of root nodules inhabiting in the rhizobia.

Contributions of plant growth-promoting rhizobacteria to sustainable agriculture and food security

Generally, farmers worldwide need new innovative ideas for farming to increase farm production that can take care of the human population, which is estimated to be approximately 7 billion globally. For food security to be actualized, it requires a process of producing adequate food and improving its quality. This process must maintain the ever-increasing human population without sabotaging environmental protection and impacting the environment negatively, this process is referred to as the global green revolution (Igiehon and Babalola 2018a). However, sustainable agricultural development is needed to ease these issues. According to National Research Council, the advancement of recent eco-friendly agricultural practices, energy conservation strategies, and natural resources that are promising to food security are the crucial goals of sustainable food production (Grafton et al. 2015; Igiehon et al. 2019).

Researchers have indicated that the most promising approaches to accomplish these objectives are to substitute harmful pesticides and inorganic fertilizers with environmental friendly symbiotic microbial formulations, for example, *Bradyrhizobium* species with the possible attribute of improving plant health and crop yields, while protecting

Table 2 Some rhizobial nitrogen-fixing genes and their predicted functions

Nitrogen-fixing genes	Functions	References
*nif*A	Particular nitrogen-fixing regulatory protein and transcriptional stimulator; regulates the expression of genes encoding accessory functions by the aid of their RpoN-dependent -24/-12 promoters and the nitrogenase structural genes	(Brink et al. 2017)
*nif*B	Protein that controls biosynthesis iron-molybdenum cofactor	(Lemaire et al. 2018)
nifD	Nitrogenase molybdenum-iron protein and forms alpha chain	(Backer et al. 2018)
nif H	Nitrogen-fixation enzyme protein	(Chauhan et al. 2015)
*nif*K	Nitrogen-fixating enzyme (nitrogenase) molybdenum to iron protein; forms beta chain	(Kuan et al. 2016)
*nif*Q	Protein that aid in nitrogen fixation and binding of molybdenum to iron	(Lemaire and Gastal 2016)
*nif*W	Stabilizes nitrogen-fixing enzyme, nitrogenase	(Srivastavia 2017)
nif X	Molybdenum-iron cluster binding protein	
nif Z	Nitrogen-fixing protein	(Srivastavia 2017)
*fix*A	Nitrogen-fixing gene, electron transfer flavor protein, and beta chain	
*fix*B	Nitrogen-fixing gene, proteins aid electron transfer flavor, and alpha chain	(Brink et al. 2017)
*fix*C	Nitrogen-fixing protein and oxidoredutase enzyme	(Kumari et al. 2019)
*fix*H	Nitrogen-fixing and cation transport gene	(Gastal et al. 2015)
*fix*J	Double component nitrogen-fixing regulatory protein and a direct positive regulator of *nif*A	(Lemaire and Gastal 2016a)
*fix*K	Expression of *nif*A, fixGHIS, and fix NOQP Ferrodoxin and FNR/CRP transcriptional activator and regulatory gene; Ferrodoxin, such as protein, control the gene for nitrate respiration and one of two stigma 54 proteins	(Backer et al. 2018)

plants from biotic stressors, for example, pests, phytopathogens, and abiotic stressors, such as drought, climate change, and different environmental pollutants (Lang et al. 2019; Lugtenberg 2015). There are reports on the identification and application of PGPR as a substitute to chemical-based fertilizers. The usage of PGPR as an alternative approach has enhanced the abundance and richness of soil microorganisms, have influenced plants health and yield positively (Babalola et al. 2007, 2021).

Bacterial (microbial) cultures are combined with chemically advanced carriers with the help of liquid or solid fermentation approaches. The bacterial isolates are alternatively integrated into plants in mixed or pure culture through seed or soil application, biological priming, and seedling dip. Again, it is the application of individual bacterial and identification of functionally appropriate rhizobiome. Their importance in promoting crop productivity is another basic and critical task since the rhizobiome is essential, thus it is a description of the plant host second genome (Babalola 2010; Beckers et al. 2017).

Therefore, to attain food security, there is a need to depend on the advancement of plant diversity, growth, and seed yield. The major way this can be accomplished is by inoculation of crops with rhizobacteria, such as *Rhizobium* species (Igiehon and Babalola 2018a; Igiehon et al. 2019), as discussed below.

The effects of rhizobial inoculant as a plant growth promoter

Rhizobium species are bacteria capable of reducing atmospheric nitrogen to ammonia through nodule formulation in the stems or roots of host plants. Due to the agricultural and environmental significance of *Rhizobium* species, many researches have been conducted on the bacteria (Ambrosini et al. 2018). The inoculation of seeds with *Rhizobium* species was recorded to improve the formation of the nodule, nitrogen absorption, and seed protein. Some seeds, such as sunflower (*Helianthus annuus* L), soybean (*Glycine max* L.), lentil, and pea inoculated with *Rhizobium* species enhanced root nodulation, root and shoot microbial diversity, seedling height, and shoot biomass, as a result, increased plant growth and crop yield significantly (Ambrosini et al. 2018). Other yield constituents included the number of seeds per pod, total number of pods per crop, and sum of branches bearing pod per plant was as well improved (Brader et al. 2017; Enebe and Babalola 2018).

In a field and greenhouse study the researchers reported that *Vicia sativa* L. plants were modified with *Azospirillium*, the result showed that there was a notable increase in nitrogen-fixing activities, N content, and percentage (Igiehon and Babalola 2018a). A similar experiment on peanut plant showed that there was an improvement in the number of root nodules, root dry weight, and plant growth. Chicken pea treated with *Rhizobium* species both in greenhouse and field experiments compared to the controls improved plant growth (Lawson et al. 2017). *Rhizobium* species were more effective on the plant growth when co-inoculated with other plant growth-promoting microorganisms. *Rhizobium* species co-inoculated with few bacterial species will not only improve the effectiveness of *Rhizobium* species but will advance crop production (Kuan et al. 2016; Lang et al. 2019).

Some beneficial bacterial species that have favorably improved crop productivity by co-inoculation with *Rhizobium* species are *Azotobacter*, *Bacillus*, *Enterobacter*, *Serratia*, and *Pseudomonas* (Ambrosini et al. 2016). The co-inoculation of *Rhizobium leguminosarum bv. trifoli* and *Azospirillium lipoferum* enhanced white clover root nodulation (Igiehon and Babalola 2018a). Furthermore, there are reports on *Rhizobium* and *Azospirillium* co-inoculation on the bean with increased nitrogen-fixing activity in the crop (Igiehon and Babalola 2018a; Lang et al. 2019; Lugtenberg 2015).

The co-inoculation of *Rhizobium* and *Bacillus* species on cowpea resulted in the bacterial species stimulating plant growth by increasing the nutrient uptake and root weight (Igiehon and Babalola 2018a; Lang et al. 2019; Lugtenberg 2015). The combination of *Bacillus, Rhizobium,* and *Azospirillium* species advanced nitrogen fixation and root nodulation in pigeon pea. The co-inoculation of *Streptomyces lylius* WYEC108 and *Rhizobium* sp. promoted the growth of pea by increasing the number of nodules. Again, enhanced the colonization of *Streptomyces* at the root and root nodules (Li et al. 2019). The combinations of various inoculants have been explored in different crop experiments but there is still a need for further research.

Another, the incorporation of *Rhizobium* sp. in crops stimulates crop growth and serves as a substitute to expensive chemical-based fertilizers too. Using relevant species as an inoculant in environments with nitrogen gas depletion can be a better avenue to improve the growth and development of crops (Igiehon and Babalola 2018a; Lyu et al. 2019). Taking in mind the inexpensive rate of inoculation and many agricultural benefits, farmers are encouraged to take advantage of the numerous benefits of these bioinoculants and biofertilizers on crops.

The effects of rhizobial inoculant on plants photosynthesis and chlorophyll concentration

Nitrogen is an essential plant regulating element for growth because it is limited in the environment. Plants require an abundance of nitrogen than other mineral nutrients for their growth. Nitrogen is a major component of many organic compounds, including proteins, chlorophylls, and plant growth regulators (Lyu et al. 2019). The visible appearance of the crop with nitrogen deficiency is stunted growth, reduced branching, and yellow colouration of the leaves. Nitrogen as a monomer of protein is essentially required for the total plant cell enzymatic processes. It is present in proteins and vitamins. Also, act as a key player in photosynthetic processes in photosynthetic plants (Zhou et al. 2016).

Plants inoculated with rhizobial strains in field and greenhouse experiments indicated a considerable increase in the chlorophyll levels of the leaves. As well, there was 80 and 140% notable increase in photosynthetic activities in plants modified with rhizobial strains compared to the controls (Xiao et al. 2017). Again, soybean inoculated with *B. japonicum* resulted in the buildup of chlorophyll content. There was an increase in diverse growth indices, such as height, number of leaves, the width of the stem, number of flowers, pod development, and root extension, which distinguished the treated plant from the control (Bulgarelli et al. 2015; Igiehon and Babalola 2018a).

Another, the impact of P and *B. japonicum* was studied in a field experiment on the growth of cowpea. Consequently, there was a drastic increase in the chlorophyll level of the leaves. However, there is still a study gap on the application of K, P, and *Rhizobium* as well as the formation of chlorophyll in *Phaseolus vulgaris,* which needs to be studied (Deng et al. 2019).

The effects of rhizobial inoculants on the mineral nutrient assimilation by plants

The availability and assimilation of mineral nutrients are important for plant growth. Mineral nutrients, such as nitrogen (N), magnesium (Mg), calcium (Ca), and potassium (K) are required by various plant varieties for their growth and increase crop productivity. The mutualistic association between *Rhizobium* species and plants can be the main N source in majority of the cropping systems, where approximately 80% of the N originating is from biological fixing of N. In a study, amendment of crop seeds with Rhizobial cultures improved N uptake and root nodulation (Deng et al. 2019; Finzi et al. 2015).

Similarly, seeds modified with *Rhizobium* spp. showed an increase in plant N from 19 to 42 mg per plant (Lange et al. 2015; Lugtenberg 2015). In a study in Brazil *Phaseolus vulgaris* amended with *Rhizobium* sp. cultures significantly increased N from about 20–60 kg per of N per hectare (Garrido-Oter et al. 2018; Igiehon et al. 2019). Potassium is another essential mineral nutrient conserved in the soil, mostly in a non-soluble form which cannot be easily absorbed by plants as a result limits plant growth. Assimilation of potassium is essential for plant function and development. For the non-soluble P form to be solubilized by PGPR, it should pass through acidification, chelation, and different enzymatic activities (Resende et al. 2014).

Mineral nutrient uptake depends on different factors, such as the interactions at the rhizosphere, the concentration of the minerals, and the ability to replace them in the soil. This challenge can be resolved by the introduction of *Rhizobium* spp or other phosphates solubilizing bacterial species, such as *Burkholderia*, *Bacillus*, *Erwinia,* and other important mineral nutrients into the rhizosphere soil (Manivanh et al. 2017; Souza et al. 2015). Apart from the inadequacies of the main mineral nutrients required by plants, micronutrients can also become limited in the rhizosphere, causing low crop production. Some of the essential micronutrients needed by plants are iron (Fe), molybdenum (Mo), zinc (Zn), and boron (B). It was recorded in a study that the amendment of Pigeon pea (*Cajanus canjan* L. Millsp) with *Rhizobium* strains inoculant relatively increase the number of available mineral nutrients in the rhizosphere as a result boosted the capacity of plant nutrient uptake (Lyu et al. 2019).

The impact of *Rhizobium* strains inoculants on the increase of minerals nutrients uptake in the rhizosphere and plant growth have been reported by authors (Igiehon and Babalola 2018a; Majeed et al. 2015b; Pii et al. 2015). A study showed the influence of *Rhizobium* strains on mineral nutrients assimilation by *Phaseolus vulgaris,* which resulted in a notable increase in Ca, P, K, S, and Mg uptake in all plant parts. The introduction of *Rhizobium* strains has improved the significant uptake of different micronutrients, including Cu, Fe, Mn, Zn, Fe, B, and Mo in various plant parts as recorded in some studies (Igiehon et al. 2019; Kuan et al. 2016).

The relationship between of PGPR, iron acquisition, crop productivity, and phytopathogens extermination for sustainable agriculture

Important mineral nutrient, such as inorganic N, Fe, and P required by plants can be acquired through symbiotic associations with rhizobacteria. Plants often absorb Fe from reduced ferrous ion (Fe^{2+}), although the ferric ion (Fe^{3+}) is readily available in the soil. Most plants have been recorded to release chelators and siderophore that attach to Fe^{3+} and aid in retaining it in the soil solution. Chelators significantly release Fe^{3+} to the root surface, where it is transformed to Fe^{2+} that is then absorbed rapidly. Grasses secrete the siderophores that are absorbed alongside Fe^{3+} across the plasma membrane (Igiehon and Babalola 2018a; Kuan et al. 2016; Lange et al. 2015; Lugtenberg 2015).

Nevertheless, few PGPR can separate insoluble Fe from the soil with the help of bacterial siderophores, therefore makes it accessible for the host plant, which is evidence that some plants can take in bacterial Fe^{3+} siderophore complexes require for their growth (Lange et al. 2015; Lugtenberg 2015). There is controversy on the benefits of bacterial Fe^{3+} siderophore complex absorption to plants iron nutrition.

Some scientists recorded that the contributions of Fe from the aforementioned sources to plants and stated that the total iron requirement is little. Although, few accepted their essential benefit contributions in calcareous soils (Igiehon et al. 2019; Lugtenberg 2015). A study showed that bacterial siderophore, such as pseudobactin and ferrioxamine B did not provide a sufficient amount of iron for plants (Igiehon and Babalola 2018a; Igiehon et al. 2019).

The bioavailability of Fe in the rhizosphere soil is reduced by obtaining Fe through PGPR siderophores, as a result, impact on the proliferation of fungi, which may be harmful to plants in soils deficient of Fe. Plants are relatively productive in soil rich in microorganisms than the soil with a low amount of microorganisms. This acknowledges the fact that PGPR helps host plants by obtaining mineral nutrients (Beckers et al. 2017; Deng et al. 2019).

Challenges applying PGPR in the field for sustainable agriculture

The technology of bioinoculation holds the potential for the future. However, several challenges are encountered in the field application of PGPR in sustainable agriculture. Few main bottlenecks need to be addressed to elevate the efficacy of PGPR inoculation in field applications. The development of recent inocula is depends on laboratory screening assays that mainly depend on PGPR mechanisms, such as nitrogen fixation, calcium phosphate solubilization, the activity of ACC deaminase, and auxin synthesis (Hristeva and Denev 2017; Sessitsch and Mitter 2015). Screening of pure culture in the laboratory with plant growth promotion potential does not result from microorganisms that can promote plant growth in the field (Mukhtar et al. 2019; Murphy et al. 2015; Prasad et al. 2019).

Unfortunately, some of these organisms with the potential of improving plant growth in the field are discarded during in vitro screening in the laboratory because their mechanisms are not fully understood. The most critical challenge is the development of PGPR-based products that can be applied commercially, coupled with the process of screening, and efficient selection of the most potential organisms (Sessitsch and Mitter 2015). Some factors are being considered when isolating, screening, and selecting PGPR. Some criteria that are considered include the competence of the host plant to adapt to a specific environment, pathogens, and climate change (Itelima et al. 2018; Salas et al. 2017).

Moreover, other means of selection and isolation are the spermosphere model. This approach is an enrichment method that employs different seed exudates that are used as a source of nutrients, for instance, the one recorded as potential nitrogen-fixing bacteria from the rice rhizosphere. Isolating promising microorganisms with the capacity to inhibit soil-borne pathogens is another essential method of selection. Therefore, the potential microorganisms should be collected particularly from soils that have suppressive effects on the specific pathogen (Purwati and Herwati 2016). Other methods include selection based on characteristics associated with PGPR, such as antibiotics and siderophore production; and activity of ACC deaminase. To solve the problem of selecting the excellent and promising strains of PGPR, there is a need for upgrading to advanced assessment systems and efficient bioassays (Sessitsch and Mitter 2015).

Another is the application of PGPR as a biological control agent against phytopathogens, such as fungal pathogens. In an experiment performed in greenhouse systems, the result showed that PGPR has the potential in controlling different phytopathogens (Hristeva and Denev 2017). This was achieved because of the controlled and consistent environmental conditions in the greenhouse throughout the planting season. Nevertheless, it is impossible to achieve a constant environmental condition in the field, where instability in the biotic and abiotic factors are very high and the rivalry between indigenous micro and macrofauna is a challenge too (Itelima et al. 2018; Schlemper et al. 2017).

However, the understanding of the previously mentioned factors can be useful in deciding the appropriate type and concentration of PGPR strains, and time of inoculation. Likewise, soil types, cropping strategies, and farm management practices that could encourage PGPR survival and increase (Itelima et al. 2018). Hristeva and Denev (2017) reported that sunflower rhizosphere soil inoculated with PGPR inocula showed that there was an impact of soil type on sunflower rhizobiome population density and structure. For those reasons, the idea of engineering the rhizosphere to improve the function of PGPR is becoming more popular (Chaudhary et al. 2020; Parnell et al. 2016; Schlaeppi and Bulgarelli 2015).

Other areas of concern are to identify the appropriate carrier and to establish more excellent composite formulations that can guarantee the survival, proliferation, and actions of PGPR in field applications. Also, concentrate on compatibility with chemical-based seed treatments. To overcome the challenges of the field application of PGPR, approaches, such as optimizing the conditions for growth before the formulation, the improvement of carriers, and application technology can be helpful (Chaudhary et al. 2020; Şeker et al. 2017).

Some farms cultivated with high-value crops are frequently fumigated with broad-spectrum biocidal fumigants that can change the structure of the biological community in the soil (Macouzet 2016; Majeed et al. 2015b). However, long-term exposure to these fumigants affects the microbial community interactions, which can be helpful in nutrients acquisition and mobilization. The biocidal fumigants are damaging to soil health and pose a challenge to PGPR inocula colonization in the rhizosphere. Plant breeding has helped achieve the green revolution, still few of the frameworks of bioinoculants have been made to combine the microbiome-based form of plant breeding to accomplish a heritable PGPR population that can improve crop productivity and food security (Hristeva and Denev 2017; Macouzet 2016).

The green revolution has revealed the negative impact of inorganic fertilizers, herbicides, and pesticides application in the soil environments. The applications of chemical-based products have led to soil damage, especially as soil contaminants. The combination of plant growth promotion and bioremediation would be an advantageous approach in solving agricultural problems globally. Besides, plotting microbiota consortia to mitigate different forms of plant growth promotion and bioremediation is an important form of this approach (Barquero et al. 2019). The production of bioinoculant for a particular soil condition, defeating environmental restrictions, training of farmers, and farmworkers on how to efficiently incorporate the bioinoculants to crops are essential in the development and deployment of many important bioinocula (Prasad et al. 2019).

The different challenges discussed must be surmounted before registering commercialized PGPR products for public use. Such as, the scaling up of fermentation conditions, large scale production of PGPR, maintaining product quality, efficacy, and stability (Bashan et al. 2016). Factors that should be taken into consideration before commercialization are cost, duration of shelf-life, ease of application, rate of colonization, and compatibility. Before deciding the commercialization of PGPR products, cost capitalization, and possible markets must be considered and studied (Itelima et al. 2018). Also, the knowledge of the levels of pathogenicity, toxigenicity, and allergenicity is of utmost importance. Studies on potential gene transfer and persistence in the environment are needed to devise means to enhance safety measures of commercial products. Categorizing the products under the proper category, either as a biocontrol agent or biofertilizer is important as well (Barquero et al. 2019; Orlikowska et al. 2017; Parnell et al. 2016).

Meta-omics techniques for identifying rhizobiomes of agricultural sustainable importance

Before the emergence of the meta-omics techniques, microorganisms were isolated and identified using the traditional or culture-based method for isolating and classifying microorganisms. This conventional method for culturing could not identify the entire microorganisms in a sample, which made approximately 99% of the microorganisms unknown. Meta-omic method captures the non-culturable microorganisms and their functions (Fadiji and Babalola 2020). The meta-omics technique as an emerging approach is used for characterizing the functional and structural genomes in a given environmental sample. It has unlocked the understanding of diverse structures and functions exhibited by microbial communities in the plant rhizosphere (Alawiye and Babalola 2019). Table 3 highlights the different methods of identifying agricultural beneficial microbial species.

The meta-omic techniques have aid in studying microbial populations at different levels and functions. Meta-omics technique include metatranscriptomics, used to differentiate the transcriptome profile of the microbial community and their interactions using mRNA sequencing and microarray applications (Vargas-Albores et al. 2019). Another is metaproteomics an approach used to classify the totality of complementary protein at a particular time in an environmental sample, results in understanding the interactions among microorganisms and microorganisms, and between plants and microorganisms (Yu et al. 2019).

Metaproteomics assists in understanding microbial protein profiles, complex metabolic pathway, and identifies the multi-functional genes of microorganisms (Adegboye and Babalola 2013; Vargas-Albores et al. 2019). Furthermore, metagenomics with the application of shotgun metagenomic analysis (Illumina MiSeq, NextSeq, and HiSeq) predicts at the gene level the entire taxonomic and molecular functions of the microbial community in an environment. Metabolomics specifically evaluates small molecules of low-molecular weight in biological systems. It is a quantitative and qualitative analytical approach used for metabolite profiling of a huge portion of metabolomes (Jansson and Hofmockel 2018; Oulas et al. 2015).

Meta-omic applications are classified as next-generation sequencing (NGS) analyzing tools. The NGS approaches build on the strength of omics tools to study plant-associated microorganisms in an agricultural environment. These meta-omics techniques have facilitated the understanding of the variations, structures, abundance, richness, and distributions of plant rhizosphere microbial communities (Adegboye and Babalola 2013; Fadiji and Babalola 2020). Aside from comprehending the properties mentioned earlier, it is as well used in identifying microbial community members with exceptional qualities and functions in the rhizosphere. Microbial communities of different plants studied using the omics approaches are sunflower, wheat, maize, sorghum, oat, cowpea, and soybean (Donovan et al. 2018; Maropola et al. 2015). Our recent study on sunflower rhizosphere and bulk soils using NGS approach (specifically, 16S amplicon sequencing technique) revealed a mean read of 86.59–99.30% for bacteria and 7.0–13.4% for archaea. In the study, the most abundant bacterial phyla were *Proteobacteria* (18–36%), *Firmicutes* (17–51%) and *Actinobacteria* (7–38%), while *Thaumarchaeota* (1–13%) and *Crenarchaeota* (1%) were observed to be the most abundant in the archaea domain (Babalola et al. 2021). Using the same sequencing technique, a study on the microbial diversity of

Table 3 Methods of identifying agriculturally beneficial microorganisms

Methods	Applications used	Functions	Limitations	Reference
Culture-based	Planting on general or selective culture media view with the aid of a different microscope, biosensor imaging	Isolate and identify agricultural important microorganisms, identified mechanisms of a cell to cell interactions, the pattern of colonization and detection phyto-stimulatory genes	Limited information; loss of unculturable microorganisms	(Fadiji and Babalola 2020)
Amplicon sequencing/targeted metagenomics	16S and 18S rRNA amplification using PCR machine, cloning or DGGE, high throughput sequencing, RFLP, FISH, confocal laser scanning microscopy (CLSM), secondary ion mass spectrometry (SIMS), biosensor or stable isotope labelling, oligonucleotide probes, bioinformatics tools and database soft wares	Extraction of specific genomes of interest from environmental and legumes samples, identifying microbial population and functional genes performing specific metabolic activity; analyze microbial structure, identification of microorganisms involves in phyto-biocontrol and macergens genes, characterizing nutrient availability, analyze AMF genome	Limited information about the genome; damaging sampling	(Jünemann et al. 2017; Oulas et al. 2015)
Whole-genome metagenomics	Shotgun metagenomics- Illumina Hiseq or Miseq, bioinformatics tools and database soft wares	Extraction of entire genomes in an environmental sample, Identify both known and novel genes and microorganisms responsible for plant-microorganisms interactions, microorganism-microorganism interactions, Identify metagenomes with potential functional and structural genes	Number of replicates is limited; require computational power	(Donovan et al. 2018; Martellacci et al. 2019)
Metaproteomics	LC/FT-ICR, 2- dimensional electrophoresis	Profiling of proteins using protein expression profile analysis	Needs computational power; comparison to transcriptomic data	(Alawiye and Babalola 2019; Hu et al. 2018)
Metabolomics	LC–MS, GC–MS, NMR, FTIR, ESI-Micro-T of MS	For identifying and characterization of both novel and known; targeted and untargeted metabolites and their specific functions, Profiling of metabolites with biological control ability against phytopathogens; assesses metagenomic pathways	Requires a few numbers of replicate and computational power; large amount of metabolites	(Lagos et al. 2015; Sabale et al. 2019)
Metatranscriptomics	mRNA sequencing and microarray applications	Screening of untargeted genome; assessment of metabolic pathways and gene expression	Few numbers of replicates; requires computational power and comparison to metagenomics data	(Alawiye and Babalola 2019; Delmont et al. 2015)

soybean rhizosphere co-inoculated with alien *Rhizobium* sp. strain R1, *Rhizobium cellulosilyticum* strain R3 and mycorrhizal consortium unveiled different classes of bacteria such as *Actinobacteria*, *Verrumicrobia*, *Cyanobacteria*, *Acidobacteria*, *Nitrospirae*, *Firmicutes*, *Planctomycetes*, *Chloroflexi*, *Proteobacteria*, *Bacteroidetes*, and *Gemmatimonadetes* (Igiehon et al. 2020).Recently, the attention of scientists is shifting from the previous Illumina system or shotgun metagenomics to the latest third-generation sequencing techniques. The most recent third-generation techniques, for example, MinION (Nanopore) and PacBio completes its reads within 4–6 h and can take up ultra-long reads of hundreds of thousand bases, unlike the Illumina system that takes days, which is the major advantage over the Illumina system. Other advantages of the third-generation techniques are that they are relatively inexpensive, affordable, portable, and user-friendly. Furthermore, no special training or equipment is required for data analysis. It can be connected to laptop or computer system, and can easily generate a microbial profile from full-length 16S or 18S rRNA gene sequence at a significant high taxonomic resolution (Pii et al. 2015; Brader et al. 2017).

However, some limitations are encountered when using the MinION (Nanopore) and PacBio, for instance, error rate and low accuracy level, which may be due to the restriction to a specific application and continuous long reads. However, these limitations can be corrected with further improvements (Fadiji and Babalola 2020). For better knowledge of the microbial variations and structures in the rhizobiome, the combination of more than one of the omics tools is to be employed; this significantly makes the meta-omics technique a fascinating technique in system biology.

Conclusion and future prospects

This review has provided detailed insights into various microbial communities and significant impact of PGPR with a more focus on the nitrogen-fixing rhizobacteria with specific roles in sustainable agriculture. The nitrogen-fixing genes of rhizobacteria can promote plant growth even when host plants are exposed to biotic and abiotic stressors, such as a prolonged shortage of water and high salinity content. The PGPR can as well act as biofertilizers that can improve soil fertility and increase crop yields, which would reduce the world-wide dependence on chemical-based fertilizers and pesticides known to have a damaging impact on the environment. Given that these biological fertilizers are inexpensive and ultimately eco-friendly.

The understanding of the PGPR mostly nitrogen-fixing rhizobacteria is required because they are significant microbial groups that propel the activities in the plant microenvironment. The knowledge of the microbial community is advancing into evolution involving integrating different disciplines and applications that are needed. Coupled with, the interrelationship of multiple disciplines in science, in-depth knowledge of the rhizosphere, and for harnessing the metabolic products. Advancements in studies are required when more advanced technologies and data analysis software is employed.

At this present time, studying the rhizosphere is an emerging field of microbiome research that is significantly progressing in the use of novel techniques, such as the fingerprinting and third next-generation sequencing MinION (Nanopore) and PacBio applications in understanding the activities of the microbial communities in the rhizosphere regions. Scientists have the challenge of quantifying the 16S rRNA or 18S rRNA or internal transcribed spacer (ITS) sequences, a Polymerase Chain Reaction (PCR) based method and the sequencing technique targets a single genome, either 16S rRNA or 18S rRNA or ITS genes that do not provide comprehensive information on the microorganism's metagenome diversity and functions.

Omic techniques have bridged the shortfalls of the conventional techniques and the phylogenetic surveys in identifying and characterizing the entire microbial genomes and the genetic features and traits that enable microorganisms to survive in the soil environments. The data obtained using the meta-omic approaches will give a broader view, the description of the microbial components, and assists in improving the methods of combating plant diseases and improving plants growth. For the most part, promote functions worthwhile in agriculture and have a favourable impact on food production globally, and increase food security.

Acknowledgements B.C.N. appreciates the National Research Foundation South Africa/ The World Academy of Science (NRF-TWAS) for PhD stipend (UID121772). O.O.B., acknowledges the National Research Foundation, South Africa for grants (UID123634; 132595) that supported research in her laboratory.

Author's contributions All authors equally contributed.

Funding National Research Foundation, South Africa, funded the work in our laboratory (UID123634; 132595).

Declarations

Conflict of interest The authors declare no conflicts of interest.

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